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Light and warming drive forest understorey community development in different environments

Running title: Forest herb trajectories under global change

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Abstract

Plant community composition and functional traits respond to chronic drivers such as climate change and nitrogen (N) deposition. In contrast, pulse disturbances from ecosystem management can additionally change resources and conditions. Community responses to combined environmental changes may further depend on land-use legacies. Disentangling the relative importance of these global change drivers is necessary to improve predictions of future plant communities. We performed a multi-factor global change experiment to disentangle drivers of herbaceous plant community trajectories in a temperate deciduous forest. Communities of five species, assembled from a pool of fifteen forest herb species with varying ecological strategies, were grown in 384 mesocosms on soils from ancient forest (forested since at least 1850) and post-agricultural forest (forested since 1950) collected across Europe. Mesocosms were exposed to two-level full-factorial treatments of warming, light addition (representing changing forest management) and N enrichment. We measured plant height, specific leaf area (SLA), and species cover over the course of three growing seasons. Increasing light availability followed by warming reordered species towards a taller herb community, with limited effects of N enrichment or the forest land-use history. Two-way interactions between treatments and incorporating intraspecific trait variation (ITV) did not yield additional inference on community height change. Contrastingly, community SLA differed when considering ITV along with species reordering, which highlights ITV's importance for understanding leaf morphology responses to nutrient enrichment in dark conditions. Contrary to our expectations, we found limited evidence of land-use legacies affecting community responses to environmental changes, perhaps because dispersal limitation was removed in the experimental design. These findings can improve predictions of community functional trait responses to global changes by acknowledging ITV, and subtle changes in light availability. Adaptive forest management to impending global change could benefit the restoration and conservation of understorey plant communities by reducing the light availability.

Introduction

Many global change drivers currently influence the organisation of plant biodiversity from the global down to the local scale (Gonzalez et al., 2016; McGill, Dornelas, Gotelli, & Magurran, 2015; Vellend et al., 2017). Plant communities are the local and dynamic assemblages of species that can respond to such changes in the environment (Cadotte, Arnillas, Livingstone, & Yasui,

2015; Götzenberger et al., 2012). Communities can respond to chronic global change drivers, such as atmospheric deposition of nitrogen (N) and climate change (Smith, Knapp, & Collins, 2009). Contrastingly, pulse disturbances from natural dynamics or the management of ecosystems additionally alter resources and conditions (Smith et al., 2009), for example in light availability (Bernhardt-Römermann et al., 2011; Fourrier, Bouchard, & Pothier, 2015; Kern, Montgomery, Reich, & Strong, 2013). Community responses to environmental changes may further depend on legacies from previous changes and in particular those of past land-use (Perring et al., 2016). Disentangling the relative importance of these global change drivers is necessary to improve predictions of plant community development in a changing world (Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012; Moran, Hartig, & Bell, 2016; Verheyen et al., 2017).

Plant communities, in terms of composition and functional trait distributions, can develop progressively in response to chronic global change drivers (Smith et al., 2009). This progressive response commences with individualistic physiological responses to environmental change (Chapin & Shaver, 1985; Smith et al., 2009). Following these individualistic responses, species in communities can "reorder", so that different species gain in dominance at the expense of other species in the community (Smith et al., 2009). Finally, species can be lost or gained from the local species pool via processes of migration (Anderson et al., 2011; Smith et al., 2009). This sequential community response can be estimated by assessing temporal change in functional traits of species, which can characterise the ecological strategies of species and individuals (Funk et al., 2017; Garnier, Navas, & Grigulis, 2016; Violle et al., 2007). Functional traits consequently vary between species, but also within species due to local adaptation or plasticity in expression depending on the growing environment (Lajoie & Vellend, 2015, 2018; Valladares, Sanzecg-Gomez, & Zavala, 2006). This intraspecific trait variation (ITV) can have important contributions to functional trait change in plant communities (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Albert et al., 2010; Bolnick et al., 2011; Siefert, 2012), especially through nonlinear relationships or complex interactions between environmental drivers (Fajardo & Siefert, 2018; Moran et al., 2016). ITV, together with species reordering, can then jointly influence the effects of plant communities on long-term ecosystem functioning (Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016; Harte, Saleska, & Levy, 2015; Suding et al., 2008).

Ecosystem responses can depend on important previous environmental changes (Ogle et al., 2015), such as persistent legacies of past land use (Bürgi, Östlund, & Mladenoff, 2017; Perring et

al., 2016). Land-use legacies are any alterations in resources and conditions of terrestrial ecosystems brought about by previous land use, and together with processes of dispersal, selection, drift and speciation can steer communities and ecosystem functions onto trajectories of change (Foster et al., 2003; Perring et al., 2016). Furthermore, land-use legacies often enforce lagging ecosystem dynamics, so that ecosystems with a slower development have more potential to be influenced by their effects (Bürgi et al., 2017). Effects of land-use legacies are consequently well-documented in temperate forests, and on community dynamics in the herbaceous understorey layer in particular (Abadie et al., 2018; Brudvig, Grman, Habeck, Orrock, & Ledvina, 2013; Hermy & Verheyen, 2007; Newbold et al., 2015; Verheyen, Bossuyt, Hermy, & Tack, 1999).

Forest land-use history can drive understorey community development and trait distributions for decades to centuries through processes of dispersal limitation and competitive exclusion (Brunet, De Frenne, Holmström, & Mayr, 2012; De Frenne, Baeten, et al., 2011; Naaf & Kolk, 2015; Naaf & Wulf, 2012). Characteristic understorey species are typically slow colonisers which constrain presence to ancient forest (Baeten, Davies, Verheyen, Van Calster, & Vellend, 2015; De Frenne, Baeten, et al., 2011). Ancient forest can be defined as continuously forested land since the earliest reliable land-use maps, not to be confused with unmanaged or pristine "old growth forest" or "primary forest" (see McMullin & Wiersma, 2019). Slow colonisers have resource conservative traits, with a low leaf area to mass ratio (specific leaf area, SLA) and a low height (Blondeel, Remy, et al., 2019; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003). Reproduction by seed is often less important to these species, as they may favour clonal reproduction (Klimešová, Tackenberg, & Herben, 2016; Verheyen et al., 2003), which inhibits colonisation. These species can perform photosynthesis in dense forests, either as spring-flowering geophytes (Mabry, Gerken, & Thompson, 2008; Rothstein, 2000; Tessier & Raynal, 2003) or as shade tolerant plants that persist in dark conditions (Valladares & Niinemets, 2008). Contrastingly, fast colonising species may be more abundant on afforested old fields or "post-agricultural forest" (De Frenne, Baeten, et al., 2011; Verheyen et al., 2003). These fast colonisers can have resource acquisitive traits with a tall stature and high SLA (Beckman, Bullock, & Salguero-Gómez, 2018; Díaz et al., 2016; Thomson, Moles, Auld, & Kingsford, 2011; Verheyen et al., 2003). Fast colonisers can benefit from a persistent legacy of large soil phosphorus stocks (P) as a result of prior fertilisation (De Schrijver et al., 2012), which can vary due to intensity of previous agricultural practices (Blondeel, Perring, et al., 2019; Macdonald, Bennett, & Taranu, 2012). Beyond edaphic site properties, past land use can determine forest understorey development which may be further modulated onto

different trajectories in response to environmental change (Perring, Bernhardt-Römermann, et al., 2018; Perring, Diekmann, et al., 2018).

Among a myriad of anthropogenic global change drivers (Fuhrer et al., 2016; Ripple et al., 2017; Steffen et al., 2015; Waters et al., 2016), three main environmental change drivers could interactively affect community development trajectories of forest understoreys in addition to the forest land-use history (Gilliam, 2007). First, intensifying forest management can increase the light availability at the forest floor by breaching canopy shade (Valladares, Laanisto, Niinemets, & Zavala, 2016). Plant community theories predict that increasing light availability can modulate the herb layer development trajectory in sites where N and P are less limiting to plant growth (Grime, 2001; Jabot & Pottier, 2012; Tilman, 1988), which has been observed in temperate forest understories (Baeten, Vanhellemont, De Frenne, De Schrijver, et al., 2010; Hedwall & Brunet, 2016). Second, this increase in light availability can accelerate effects of climate warming so that herbaceous communities come to resemble those of warmth-adapted communities (Bjorkman et al., 2018; De Frenne et al., 2015; Helsen et al., 2017; Henn et al., 2018; Hoeppner & Dukes, 2012). The increasing light availability may also alter soil microbial communities and enhance their activity which can release nutrients for plants (Ma et al., 2018; Ni et al., 2018). Third, N enrichment from atmospheric deposition (Bobbink et al., 2010) can enhance plant growth (Fraterrigo, Pearson, & Turner, 2009; Hejcman, Křišťálová, Červená, Hrdličková, & Pavlů, 2012; Siefert & Ritchie, 2016), and can change community composition by increasing the abundance of nitrophilic species when light availability is high (Dirnböck et al., 2017, 2014; Gilliam et al., 2016; Walter, Adams, Gilliam, & Peterjohn, 2017).

Here we assess trajectories of forest understorey communities in response to enhanced light availability, warming and N enrichment. We performed these treatments in a full-factorial experiment on artificially assembled plant communities comprising species with varying ecological strategies, on ancient and post-agricultural forest soils. This setup allows us to assess effects of agricultural legacies on communities unaffected by dispersal limitation (see also Barker et al., 2019). We hypothesise:

1. **Community response driven by species.** Species can reorder in response to environmental treatments, leading up to changes in community composition and species richness declines (given that increases are not possible in the experimental design). We expect contrasting development trajectories of communities due to species-specific

responses to the forest land-use history and treatments of light addition, warming and N addition.

2. **Community response in functional traits.** Species reordering can change functional traits averaged across the community. In addition, intraspecific trait variation (ITV) can co-determine functional trait distributions in communities. We expect that communities change towards higher dominance of taller plants with higher SLA where environmental limitation is alleviated due to multiple environmental treatments. Concretely, we examine evidence for two-way interactions between light addition, N enrichment, warming and agricultural land-use history on change in community-mean plant height and SLA.

Materials and Methods

We performed a full-factorial experiment with 384 experimental units (mesocosms) to disentangle effects of forest land-use history, enhanced light availability, nitrogen addition and warming on plant communities assembled from fifteen common European herbaceous species. The experiment started in April 2016 and data collection for this analysis ended in August 2018. We measured plant height values from 3445 individual plants and characterised SLA using 1125 leaf samples at the halfway point in the experiment (the growing season of 2017). We calculated two community weighted mean trait metrics on these values; one metric incorporates intraspecific trait variation (ITV) and one uses a single average trait value per species.

Land-use legacies: ancient and post-agricultural forest soils across environmental gradients

This mesocosm experiment used soil from eight environmentally contrasting regions in temperate Europe to increase the generality of the results (Blondeel, Perring, et al., 2019; Verheyen et al., 2017). Regions spanned from Southwest Estonia (N 58 ° 8' 45.10", E 24° 47' 04.83") to Central France (N 47° 50' 10.04",E 2° 45' 39.80") and included Southern Sweden (N 55° 32' 58.67", E 13° 14' 28.11"), Northwest Germany (N 53° 20' 25.12", E 9° 25' 17.34"), Northeast Germany (N 53° 13' 41.41", E 12° 07' 30.06"), Northern Belgium (N 51° 00' 00.30", E 4° 20' 17.13"), Southern Belgium (N 50° 03' 56.05", E 4° 22' 01.54") and Northern France (N 49° 53' 42.65", E 2° 18' 41.36"). These regions differ in inherent soil fertility, regional phosphorus balance and nitrogen

deposition (further details in Blondeel,Perring, et al., 2019). The collected soils were classified in three groups (using cluster analysis) according to inherent characteristics (texture and calcareous properties). These groups were either i) relatively rich in clay and carbonates with high base saturation ("eutrophic'), ii) relatively high in sand and relatively low pH and base saturation ("oligotrophic") or iii) intermediate fertility with siltier textures and intermediate base saturation ("mesotrophic") (see Blondeel,Perring, et al., 2019, Supplementary Table S1.1). We had applied these terms to denote the poorest soils ("oligotrophic") vs intermediately rich ("mesotrophic") and richest soils ("eutrophic") in our samples, and not to compare them outside our population. We use the region as a random effect term and the categorical soil type variable as a covariate when analysing data using linear mixed-effects models (see section "Data analysis").

To enable a comparison by land-use legacy, we searched for three adjacent stand pairs of ancient and post-agricultural broadleaved forest with similar canopy composition per region, leading to 48 forest patches included in the study (Blondeel, Perring, et al., 2019). We selected pairs of forest patches (median distance: 760 m) with similar stand age, where one patch was in existence before 1850 (ancient forest) and the other forested in the mid-20th century (post-agricultural forest). We are consequently able to account for the effects of forest land-use legacies, i.e. alterations to soil biogeochemistry driven by past land use. Adjacent stand pairs had the same soil type classification in 21 out of 24 pairs, with the other three having a richer class on post-agricultural soil but similar classifications from the Soil World Reference Base (Supplementary Table S1.1). We collected the soil from a pit with a surface area of 1 m x 0.7 m, and a depth of 0.15 m (ca 0.1 m³ per forest patch). Overall, the soils from post-agricultural forest had higher pH (+0.4 ± 0.16 standard error (S.E.)), lower C:N (-1.49 ± 0.24 S.E.) , higher total P concentration (+118 mg kg^{-1} soil ± 60 S.E.) and higher Olsen P concentration (+13 mg kg^{-1} soil ± 5.5 S.E.) compared to ancient forest (Blondeel, Perring, et al., 2019).

We transported all 48 collected soil samples to the long-term ecological research site (LTER) in the Aelmoeseneie forest in Belgium during November 2015- February 2016 (50°58′30" N, 3°48′16" E, mean annual temperature (MAT) = 10.6 °C, mean annual precipitation (MAP) = 768 mm, altitude = 20 m, N deposition (2016) = 15.5 kg N ha^{-1}) (DEIMS-SDR Database). The sampled soil from each forest patch was divided over eight mesocosms, one for each two-level

factorial combination of light x warming x temperature. Each mesocosm (46.5 x 31.5 cm, 19 cm depth) consisted of 13L soil on top of 9 L of white sand to ensure proper drainage.

Plant community assembly: slow and fast colonisers grow together

We compiled a pool of fifteen species commonly found in temperate European forests (supplementary Table S1.2) and divided this species pool into three categories that accounts for a species' affinity to ancient forest based on our own expert knowledge. We based our classification on studies that had characterised typical ancient forest species in relation to a species' colonisation capacity (De Frenne, Baeten, et al., 2011; Verheyen et al., 2003) and habitat use as a forest specialist (Heinken et al., 2019). The first group (A) are six poor colonisers and forest specialists, typically of ancient forest (Supplementary Table S1.2). The second group (B) are six common intermediate colonizers of post-agricultural forest and not strictly forest specialists (Supplementary Table S1.2). The final group (C) are three fast colonising and generalist nitrophilic species (Supplementary Table S1.2). The classification is consequently not on the colonisation capacity index (CCI) alone. For those reasons, *Polygonatum multiflorum* is in group A as it is a typical forest species. Likewise, group B incorporates species with a wider range in habitat use and are not strictly forest specialists. *Ajuga reptans* and *Poa nemoralis* can occur in grassy habitats and grasslands, while *Hedera helix* is often found in urban and rural habitats.

We assembled twelve communities (Supplementary Table S1.3) in which we randomly assigned two poor colonisers (group A), two intermediate colonisers of post-agricultural forest (group B) and one fast-colonising nitrophilic species (group C). These twelve plant community combinations serve as representative species assemblages in temperate mesotrophic deciduous forests in Europe. Each species occurs in four different assemblages. The twelve communities are repeated four times over the 48 soil samples in each two level factorial combination of light x warming x nitrogen addition (48 soil samples x 8 factorial combinations = 384 mesocosms). Repetition of communities was randomised using the "sample" function in R (R Core Team, 2019). Communities were allowed to differ on a given pair of a soil sample (i.e. paired post agricultural vs ancient forest soil) in a given environmental treatment in the randomisation processes. The randomisation restricted the same species combination occurring multiple times on the same soil origin to avoid confounding of any soil type effect with a particular plant community.

We prepared the planting of the 384 mesocosms in the first week of March 2016. Each of the five species in a community were planted four times per mesocosm in a grid (7x8.5 cm) in a randomised order, resulting in 20 plants per mesocosm. We installed all mesocosms in a fenced area in the Aelmoeseneie Forest (Belgium) with a tree canopy (95% cover) dominated by *Fagus sylvatica*, *Quercus robur, Acer pseudoplatanus*, *Fraxinus excelsior* and *Larix decidua.* We buried mesocosms in random groups of four ("plots") to apply manipulative experimental treatments, as explained in the next section and following methods of De Frenne et al. (2015). In total, we planted 7680 individuals (384 mesocosms x 20) of fifteen species (512 individuals per species).

Manipulating the environment: N enrichment, experimental warming and enhanced light availability

We have applied three two-level environmental treatments in a full-factorial design since April 2016. Ongoing treatments consist of (i) nitrogen enrichment; (ii) experimental warming and (iii) enhanced light availability. The first treatment is N enrichment (further referred to as treatment "N") by adding 0.25 L of a 2.01 g L-1 solution of NH_4NO_3 (50 kg N ha^{-1} yr^{-1} eq.) per mesocosm and rinsing the leaves with 0.25 L of demineralised water. We performed this treatment four times per year at the start of each season, with the control mesocosms receiving 0.5 L of demineralised water. The second treatment consisted of experimental warming (referred to as treatment "T") with 75 cm-wide open top chambers (De Frenne et al., 2010). We measured air temperature (15 cm above forest floor), surface temperature (0 cm) and subsurface soil temperature (5 cm depth) in eight plots, one for each factorial combination of light x warming x nitrogen, using 24 thermocouples which log every 30 seconds (Type T miniature, TC Direct, The Netherlands and datalogger type CR1000, Campbell Scientific, USA). The warming effect of the open top chambers fluctuated throughout the two calendar years in which we recorded temperatures (2017 – 2018), with the largest increases in monthly air temperatures (15 cm above soil surface) during April in both 2017 (+1.73 °C ± 0.54 S.E.) and in 2018 (+2.00 °C ± 0.69 S.E.). This time of year is optimal for passive warming with open top champers, as the forest canopy is not yet developed but solar radiation becomes more intense (De Frenne, Brunet, et al., 2011; De Frenne et al., 2010; Pelini et al., 2011). We recorded less pronounced warming effects at surface level (0 cm) and in the soil at 5 cm depth (Supplementary Fig. S1.1). The third treatment, light addition (referred to as

"L"), adds 23.98±4.40 µmol $m^{-2}s^{-1}$ PAR to the ambient light conditions (7.79±0.68 µmol $m^{-2}s^{-1}$ under fully closed canopy) at 15 cm high. We used two 18 W fluorescent tubes suspended 75 cm above ground level of each plot. These lights are programmed to follow the natural photoperiod throughout the year and did not significantly affect air temperatures (De Frenne et al., 2015). This increment in light availability can be associated to a small forest gap, and could increase carbon assimilation rates in typical forest understorey plants by three times (Rothstein & Zak, 2001).

Summarising the design of the 384 mesocosms, we have eight regional origins of soil (classified in three groups according to inherent soil fertility), with three ancient and three post-agricultural forest soils (LU) in each region (48 soil samples), using two-level factorial treatments of N enrichment (N), warming (T) and light (L) addition (8 combinations).

Plant trait and community measurements

We measured plant height and SLA in the second growing season of the experiment, from March 2017 to September 2017, at the time of each species' estimated biomass peak (Supplementary Table S1.1, Table S1.2). These measured trait values can thus denote the fitness of each species in the different treatment combinations (Garnier et al., 2016), 16 in total for T,L,N,LU combinations. We consequently have multiple trait measurements within each species in the different treatment combinations, but not at a different time point, so that ontogeny or growth are not taken into account. We chose not to measure reproductive traits (i.e. seed mass) as proposed in the common leaf-height-seed ecological strategy scheme (Laughlin, Leppert, Moore, & Sieg, 2010; Westoby, 1998). Several herbaceous species in our pool favour clonal reproduction, so that seeding is often limited in these species (Klimešová et al., 2016). Sexual reproductive traits within and between species can also have ambiguous responses to multiple environmental drivers (Garnier et al., 2016). Furthermore, these reproductive traits can be intensive to correctly measure and quantify given our large numbers of test plants (Pérez-Harguindeguy et al., 2013).

We were able to measure plant height on the 3445 survivors of the 7680 initially planted individuals (44%).Vegetative plant height (unit: m) was measured as the shortest distance between ground level and the upper boundary of main photosynthetic tissues. This means that we solely measured foliage height, not inflorescence or seeding height (Pérez-Harguindeguy et al., 2013).

We measured average specific leaf area (SLA) as the one-sided area of multiple leaves from a single species in each mesocosm, divided by the oven-dry mass and expressed in $mm^2\ mg^{-1}$ (Pérez-Harguindeguy et al., 2013). We collected maximally eight leaves of each species per mesocosm and no more than two per individual to avoid excessive damage to any individual plant. We collected fully expanded leaves from adult plants (which emerged in growing season of 2017), but not including a petiole where present. We avoided leaves with pathogen or herbivore damage and only sampled outer leaves (Pérez-Harguindeguy et al., 2013). The projected area of the leaves was measured with the *Easy leaf area free* mobile application (Easlon & Bloom, 2014) within two hours of picking the leaves, after taking a picture of the leaves with a mobile phone (13 MP camera). This open-source software package can estimate green leaf area in a RGB photograph by counting the total amount of green pixels and converting this into an area measurement by counting red pixels from a 4 cm^2 calibration square provided in the image. After the area measurement (mm^2), each leaf sample was dried in an oven at 65°C for 48 hours to ensure constant mass upon weighing (in mg).

In order to calculate an abundance weighted mean trait value for the community, we estimated species cover in all mesocosms at seven instances between May 2016 and August 2018. In 2016, we visually estimated the percentage cover of each species in each mesocosm in the field during the second week of May (11th May, 1 month since start of experiment), in the first week of July (6th July, after 3 months) and in the second week of September (12th September, after 5 months). To spread this labour intensive effort more efficiently over the year, we subsequently modified our method. With this modification, we first measured the total vegetation cover since 2017 using digital images. We took digital RGB photographs of the mesocosms perpendicular to the ground surface at two time points in 2017, during the first week of May (4th May, after 13 months) and the second week of August (11th August, after 16 months). We repeated this process in 2018, during the first week of May (7th May, after 25 months) and the second week of August (10th August, after 28 months). These images were analysed using the "Canopy Area" tool that measures green pixels of vegetation and recalculates this into a cover percentage (Easlon & Bloom, 2014). From these images, we visually estimated each species share of the total vegetation cover.

Data analysis

All data analysis was performed in R (R Core Team, 2019). We used the package nlme (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2018) to calculate linear mixed effects models.

In the first hypothesis, we test whether warming (T), enhanced light availability (L), N addition (N) and the forest land-use history (LU) altered community trajectories in terms of species loss and species reordering as main effects. We first tested whether species richness changed from May 2016 until August 2018 at the seven recorded time points, depending on two-way interactions of year (Year) with T, L, N, LU and of season (spring vs summer) in two-way interaction with T,L,N,LU. We therefore applied a consistent random effects structure including separate random effects of region (8 levels), species combination (12 levels) and the group of four mesocosms i.e. "plot" (96 levels). We tested these predictors in one generalised linear mixed effects model (Poisson error distribution) with our invariable set of random effect terms using the *glmmPQL* function from the *MASS* package (Venables & Ripley, 2002), with a t-test provided by the summary output (estimates and standard errors, Supplementary Table S1.4).

To test the species reordering over time in response to the four treatments, we performed a principal response curves (PRC) analysis (Van den Brink & Ter Braak, 1999) on the seven recorded time points between May 2016 and August 2018 using the "prc" function in the vegan package (Oksanen et al., 2019). The PRC method is based on redundancy analysis (RDA) and allows estimating which species gain in abundance at the expense of others in response to the treatment and with "time" as an explicit factor. The graphical output shows abundance changes over time in the control treatments transformed to a flat zero reference line (x-axis) while abundance change in the treatment is allowed to deviate from this reference (van den Brink, den Besten, bij de Vaate, & ter Braak, 2009). The accompanying species scores (right hand y-axis) can be multiplied with the canonical coefficients of the partial RDA (left hand y-axis), which yields the proportional increase or decrease of a species in the treatment compared to the control (*100 for a percentage change). Species with large negative scores increase with the treatment, while species with positive scores decrease in abundance relative to the control. Species scores within 0.5 distance of zero indicate little abundance change in response to the treatment. The significance

($p < 0.05$) of the PRC is tested by performing a Monte Carlo simulation (10 000 permutations) of the time series, using ANOVA (F-test) which evaluates the first axis of the partial RDA.

In the second hypothesis, we test whether cover-weighed community weighted means (CWM) of plant height and specific leaf area (SLA) change over time in response to two-way interactions of T, L, N and LU. We selected the difference between the situation in May 2016 (first spring recording) and May 2018 (last spring recording). Mid spring (end of April/early May) is the time of year with maximal community biomass with all species present, and has traditionally been the time for performing forest understorey vegetation surveys (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999; Peterken, 1974). We calculated two CWM measures from these cover abundances: one that ignored within-species variation in trait values (a "single species-single trait value" approach, CWM_{single}), and a CWM where we account for different trait values within species due to the array of growing environments in the experimental setup (CWM_{ITV}). CWM_{single} simply uses the average measured trait value of a species across all mesocosms to calculate a CWM (Supplementary Table S1.5), and can only change when species reorder in abundance. We weighted these species trait values by the species covers in a given mesocosm at a given time, divided by the sum of those species covers. CWM_{ITV} applies the same abundance measure, but instead uses one of 16 average trait values for each species depending on the factorial combination of the two-level T, L, N and LU treatments (16 combinations, see Supplementary Table S1.5). CWM_{ITV} can consequently differ due to species reordering and ITV together. To infer the amount of variation that species reordering explains in community trait responses, we calculated an R^2 value between CWM_{single} and CWM_{ITV} as the squared value of the Pearson's correlation coefficient between these two variables. The higher the R^2 value, the more that species reordering explains the community response.

We then calculated community change over time as log response ratios, i.e. the natural logarithm of the CWM in May 2018 over the CWM in May 2016, for both CWM_{single} and CWM_{ITV} and as a function of two-way interactions between warming (T), light availability (L) and N enrichment (N) and the forest land-use history (LU, ancient forest as intercept). We performed backwards variable selection using the *drop1* function (R Core Team, 2019), where in each step the interaction with the highest p-value on a Chi-squared test is dropped from the model. This initial model structure includes all main effects (T, L, N, LU), all two-way interactions (T:LU, N:LU,

L:LU, T:N, T:L, L:N) , a fixed-factor covariate Soil type (3 levels), and the random effect terms (Region (8), species combination (12), plot (96)). The final model, after stepwise deletion of insignificant interactions, includes all main effects and any interaction term with associated p values smaller than 0.05. We evaluated model residuals against normality with a qq-plot of the models, which all had acceptable agreement between observed and theoretical quantiles within two standardized quantiles around zero. We also checked the model plots of residuals vs fitted values to check for inconsistencies given the factors included in the model, which we did not observe.

Results

Looking at compositional change (hypothesis 1), we found that species richness in the mesocosms decreased as expected over the course of three years with on average one lost species per year (Fig. 1a, Supplementary Table S1.4). We planted the experiment at March 2016 with five species, but the mean species richness in mean May 2016 was already four species (4.1, 95% CI [3.8; 4.4]). Within-season variability occurred due to the presence of vernal species, with summer surveys having one less species on average than the spring surveys in the first year (3.0, 95% CI [2.7; 3.4]), a trend that persists in Year 2 and 3 as well (Fig. 1a). Estimates of mean species richness and the time variables did not significantly differ on the 95% confidence interval depending on warming (T), light addition (L), N addition or the land-use history (LU) of the soil (Fig. 1b).

We tested the reordering of species in the treatments using principal response curves (PRC). Separate PRC of light (L), warming (T), N addition (N) and the forest land-use history (LU) treatments revealed that only the light treatment ($p < 0.05$) had significant effects on species reordering over time (Fig. 2a). Warming had evidence for a minor significant effect ($p = 0.06$, Fig. 2b), while N addition ($p = 0.97$, Fig. 2c) or the forest land-use history did not ($p = 0.23$, Fig. 2d). Proportional abundance changes of species in the light treatment in comparison to unlit controls showed that three species increased heavily in abundance with the light treatment. These increasing species were *Carex sylvatica* (+243%), *Galium odoratum* (+120 %) and *Polygonatum multiflorum* (+72 %). In contrast, we found that *Hyacinthoides non-scripta*, (-38%), *Ficaria verna* (-36%) and *Anemone nemorasa* (-18%) decreased in abundance when light was applied in any treatment combination (Table 1).

Table 1: Proportional abundances changes (%) of each species after 25 months (May 2018) in the light treatment compared to the change in the controls in the same time period. These abundance changes are illustrations to the significant principal response curves of the light treatment found in Fig. 2a. The proportional abundances changes are calculated as the species score multiplied by the canonical coefficient at month 25 (multiplied by 100 for percentage). Species with positive abundance change values increase with the light treatment, species with negative values increase in the unlit control conditions.

Species	Abundance change (%) due to light treatment
H.non-scripta	-38
F.verna	-36
A.nemorosa	-18
V.minor	-1
P.trivialis	2
A.podagraria	3
G.hederacea	3
H.helix	5
A.reptans	5
U.dioica	27
G.robertianum	44
P.nemoralis	58
P.multiflorum	72
G.odoratum	120
C.sylvatica	243

To test the second hypothesis, we applied a functional perspective to community change and tested log response ratios of CWM plant height and SLA in function of two-way interactions between treatments. The estimate of log RR for plant height in response to light is positive in the two CWM measures (Fig. 3, Supplementary Table S1.6), but slightly larger in CWM_{single} (+0.19± 0.04 S.E., $p < 0.001$) than in CWM_{ITV} (+0.15± 0.05 S.E $p = 0.002$). The estimate of plant height change to warming measured by CWM_{single} (+0.16± 0.04 se, $p < 0.001$) is also larger than CWM_{ITV} (+0.10± 0.05 se, $p = 0.04$). These positive plant height changes due to light and warming

are also evident when looking at the CWM trait values directly rather than equating the change with the log RR (Fig. 4a,b). Overall, the shared variance between CWM_{single} (change driven by species reordering) and CWM_{ITV} (change driven by species reordering and ITV) of plant height was high ($R^2 = 0.76$).

CWM_{single} and CWM_{ITV} of SLA yielded different significant responses to the environmental treatments (Fig. 3, Supplementary Table S1.6). Light had a significant positive effect on log RR of CWM_{single} (+0.08 ± 0.02 S.E., $p = 0.002$), driven by some outlier points (Fig. 4c). Contrastingly, log RR of CWM_{ITV} SLA showed a significant interaction between N addition and the forest land-use history (Fig. 3) and another interaction between N addition and the light treatment (Fig. 3). These interactions result from variation in CWM_{ITV} SLA at the initial survey, which converged towards the mean SLA after three years (Fig. 4d). The variability that ITV causes in community SLA is also evident from the lower shared variance, in comparison with plant height, between CWM_{single} (only driven by species reordering) and CWM_{ITV} (driven by species reordering and ITV). The shared variance between CWM_{single} and CWM_{ITV} is 42 % ($R^2 = 0.42$), so that 58 % of the variation in CWM_{ITV} is caused by using different trait expressions of species depending on the treatment combination.

Discussion

We found that light and warming were prominent drivers for diverging plant community trajectories in our mesocosm experiment, more than N enrichment and the forest land-use history. Interactions between treatments were rarely important for explaining variation in community trait change. The light treatment modulated abundance changes in the herbaceous communities over time so that species reordered, with spring geophytes as winners in unlit conditions. Species in communities reordered towards taller plants when illumination and warming were applied. Increasing plant community height was three quarters driven by species reordering, with leftover variation accounted for by intraspecific trait variation (ITV). In contrast, responses of community SLA differed when considering ITV in comparison to the effects of species reordering only. These findings show the importance of ITV for leaf morphology responses to nutrient enrichment in dark conditions. Incorporating ITV in community SLA is thus necessary to make accurate predictions in future global change scenarios, but less important for plant height. An important and unexpected result of our experiment was the limited role of interactions between global change

treatments and agricultural legacy in community development, given the expectation of evidence for its importance in observational studies (Hermy & Verheyen, 2007; Newbold et al., 2015; Perring et al., 2016).

Light availability drives development trajectories of understorey communities

Multiple studies have shown that light availability is an important trigger for community responses to nutrient enrichment and global change (Hautier, Niklaus, & Hector, 2009). This viewpoint stems from classical theoretical ecology, where competition for light is predicted when N and P are less limiting, which can lead to species loss (Chapin & Shaver, 1985; Freckleton & Watkinson, 2001; Grime, 2001; Lonsdale & Watkinson, 1982; Tilman, 1990). We did not find species loss due to treatments in our experiment, but rather an average loss across all treatments of two species after three growing seasons. Instead of nutrient availability, light was by far the limiting resource due to the dense tree canopy in our experimental site, which influenced abundance changes in the communities. While the PAR increments in the enhanced light availability treatments were subtle, they could be enough to already increase carbon assimilation rates in these understorey species by a third of the light saturation point (Rothstein & Zak, 2001). The importance of climate-buffering canopy shade is indeed recognised to be key in understanding understorey plant ecology in the face of global change (De Frenne et al., 2019; Landuyt et al., 2018; Valladares et al., 2016; Zellweger, De Frenne, Lenoir, Rocchini, & Coomes, 2019).

We found a larger abundance of taller plants in response to light availability and warming, which follows a recurring trend in plant communities across the globe (e.g. Bjorkman et al., 2018). Short-term experimental data show that enhanced light availability in temperate forests can accelerate plant responses to warming by steering the community towards taller warmth-adapted species (De Frenne et al., 2015). Similar community trajectories have also been observed over the course of decades using forest vegetation resurveys (Bernhardt-Römermann et al., 2015; Perring, Bernhardt-Römermann, et al., 2018; Verheyen et al., 2017). Furthermore, this trend of a taller vegetation with warming was not restricted to forest areas, but has also been observed in the faster warming tundra biome (Bjorkman et al., 2018; Myers-Smith, Thomas, & Bjorkman, 2019). The height increase in tundra communities is attributed to species turnover rather than intraspecific trait variation (Bjorkman et al., 2018; Steinbauer et al., 2018), which matches the observations in our forest

understorey experiment. Changes in other traits of tundra communities, including SLA, were reported to lag behind the predicted rates of change (Bjorkman et al., 2018; Myers-Smith et al., 2019). We too observed this unpredictability in community SLA due to a large importance of ITV. Species reordering alone led to a minor positive response of community SLA to illumination (but driven by some outliers), while the community SLA that accounts for ITV responded positively to N addition on post-agricultural forest soil and with light addition. This discrepancy in community SLA response due to ITV can occur in dark temperate forest, as light and nutrient acquisition are two different aspects of resource acquisition that influence SLA within and between species (Firn et al., 2019; Smart et al., 2017).

Our results suggest that ITV is important for understanding short-term and local community responses to environmental change (Albert et al., 2011; Moran et al., 2016), but depending on the trait of interest. Functional traits that can have complex responses to resource availability should consider ITV on the community level, such as in our observed patterns of SLA. Using a single mean trait value for each species may however be used to calculate a community trait response for traits when species turnover dominates the community response, such as for plant height. This approach is popularised by virtue of large collaborative trait databases (Kattge et al., 2011; Kleyer et al., 2008; Muscarella & Uriarte, 2016; Pérez-Harguindeguy et al., 2013). In our experiment, we could characterise the driving species for the community plant height response. These were *Carex sylvatica*, *Polygonatum multiflorum* and *Galium odoratum*, which increased in abundance with light addition. These species are characterised as relatively tall species in our species pool (Supplementary Table S1.4), but they are not considered as fast growing resource acquisitive species but rather typical of ancient forest (Wulf, 1997). These shade-tolerant species also show higher intraspecific SLA values in low light conditions for more optimal light acquisition (Blondeel et al., conditionally accepted; Liu et al., 2016; Valladares & Niinemets, 2008). Incorporating ITV on top of species reordering can thus improve predictions of future plant communities, especially with the acknowledgment of the role of light availability in community trait responses to global change.

Interacting environmental change and land-use legacies: only time can tell

We designed this multi-factor experiment to disentangle potential interactive effects of enhanced light availability, warming, N enrichment and the forest land-use history on development of forest understorey communities. Multiple examples of such interactive effects on development of understorey communities consequently exist. Warmth-loving species can increase in abundance in bright and warm forest gap conditions, with light as the accelerating driver for this warming response (De Frenne et al., 2015). Likewise, the dominance of nutrient demanding species can increase under enrichment of N and P when light availability is high (Fraterrigo, Pearson, & Turner, 2009; Gilliam et al., 2016; Holmes & Matlack, 2017; Siefert & Ritchie, 2016; Walter et al., 2016). We thus had expectations of interactive effects between the treatments in our experiment given the previous evidence.

Against our expectations, this short-term mesocosm experiment barely revealed any interactive effects between the multiple treatments on community responses. This lack of interaction on the short-term does not imply that such interactive effects are not important to understorey community development in response to global change. It rather shows the complementary of experimental research to long-term vegetation resurveys (Perring, Bernhardt-Römermann, et al., 2018; Perring, Diekmann, et al., 2018; Verstraeten et al., 2013) or mechanistic modelling approaches (Dirnböck et al., 2017; Landuyt et al., 2018). Long-term experiments, vegetation resurveys and modelling are perhaps better suited to unravel such long-term interactive effects between global change drivers on understorey communities (Luo et al., 2011; Verheyen et al., 2017). Most probably, interactions between the treatments in this experiment could emerge after prolonged time when resources and conditions other than light become more limiting (Oliver & Morecroft, 2014).

Besides the short-term nature of the experiment, the unexpected lack of a land-use legacy effect on community development could be particularly driven by the factorial experimental approach and the designed community assembly. We acknowledge that a binary land-use history classification increases orthogonality but might obscure nuances in legacy effects (Bürgi et al., 2017), as the agricultural legacy could rather exist on a gradient related to the intensity of previous agricultural practices. We performed a post-hoc analysis to investigate this possibility (see Supplementary Section 2), using the difference in bio-available phosphorus (Olsen P) between pairs of post-

agricultural and ancient soil origins as a proxy for the intensity of prior fertilisation practices (Blondeel, Perring, et al., 2019). This additional analysis confirmed a general lack of a land-use legacy effect linked to past fertilisation on community trajectories. For now, our full-factorial experiment with introduced species may not be able to reveal such long-term effects on community development. This experimental design does however allow the interpretation of land-use legacy effects without dispersal limitation as a driver for community assembly (see also Barker et al., 2019), as we bypassed dispersal by planting communities in selective combinations. The disentangled view on community development points towards an important role of light availability, followed by warming, in short-term community response to global change.

Reducing light availability is key to restore forest understoreys under global change

Similar experimental results have shown that the establishment of introduced woodland flora is not reduced in post-agricultural forest on the short-term (Barker et al., 2019) nor on longer terms (Baeten & Verheyen, 2017), when forest canopies are relatively undisturbed. Our findings thus support the notion that adaptive management to global change can restore small statured spring-flowering geophytes with high conservation priority in post-agricultural forest, but only when light is a limiting resource to enable coexistence with other species (Vandekerkhove, Verheyen, & De Keersmaeker, 2011; Verheyen et al., 2003). A structurally rich forest with a dense shrub layer can easily develop on former agricultural land over the course of a few decades to provide such a suitable forest microclimate (De Schrijver et al., 2012; Fridley & Wright, 2018; Sercu et al., 2017). The only remaining condition for settlement of slow colonising spring-flowering geophytes is then to alleviate dispersal limitation (Baeten et al., 2015; Barker et al., 2019). This can be achieved by increasing habitat connectivity between source populations (Brunet & von Oheimb, 1998; Naaf & Kolk, 2015) or by reintroductions from the local species pool (Bucharova, 2017; Drayton & Primack, 2012; Godefroid et al., 2011; Seddon, 2010). The latter action resembles the community assembly in our experiment, with mixtures of slow colonising spring-flowering geophytes and fast colonisers on both ancient and post-agricultural forest soils. Transplanting or sowing spring-flowering geophytes is, however, currently a management strategy that has rarely been put into practice beyond experimental forest ecology (e.g. Baeten & Verheyen, 2017; De

Frenne, Brunet, et al., 2011; Lajoie & Vellend, 2018; Van Der Veken, Rogister, Verheyen, Hermy, & Nathan, 2007; Yang et al., 2018).

Conclusions

We found that light availability and warming reordered species towards a taller herbaceous community, with limited effects of N enrichment and the forest land-use history. Interactions between treatments and ITV were unimportant for the plant height response. Contrastingly, community SLA differed when considering ITV along with species reordering, which highlights ITV's importance for understanding responses of leaf morphology to nutrient enrichment in dark conditions. Incorporating ITV on top of species reordering can thus improve predictions of future plant communities. Furthermore, subtle differences in light availability can yield large community trait responses to global change. This insight provides perspectives for adaptive management to global change, and demonstrates that reducing light availability is key for understorey restoration and conservation in a changing world.

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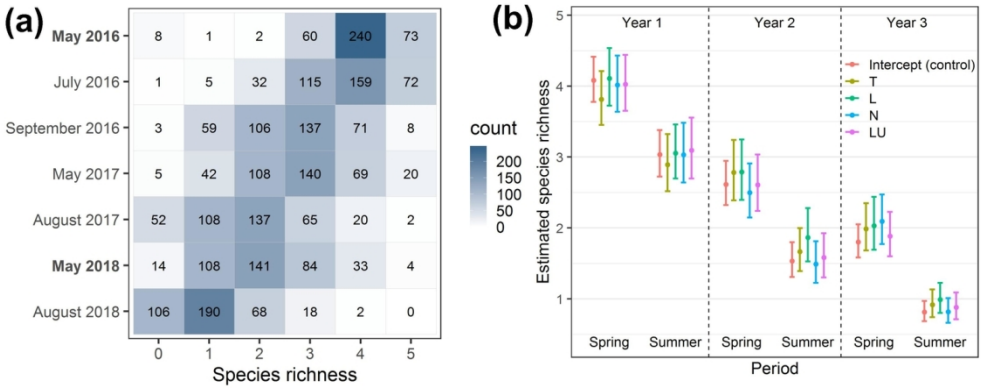

Figure 1: Species richness declined across all treatments, with one less species on average per year and one fewer species in summer months. Frequencies of mesocosms (A, inside the tiles) show declining species richness across all treatments over the course of three growing seasons. Summer (July – September) had one less species than spring (May) surveys, due to the presence of spring ephemerals. There are no significant differences in estimates of mean richness between main effects of treatments (B), while the temporal variation in species richness is clearly significant.

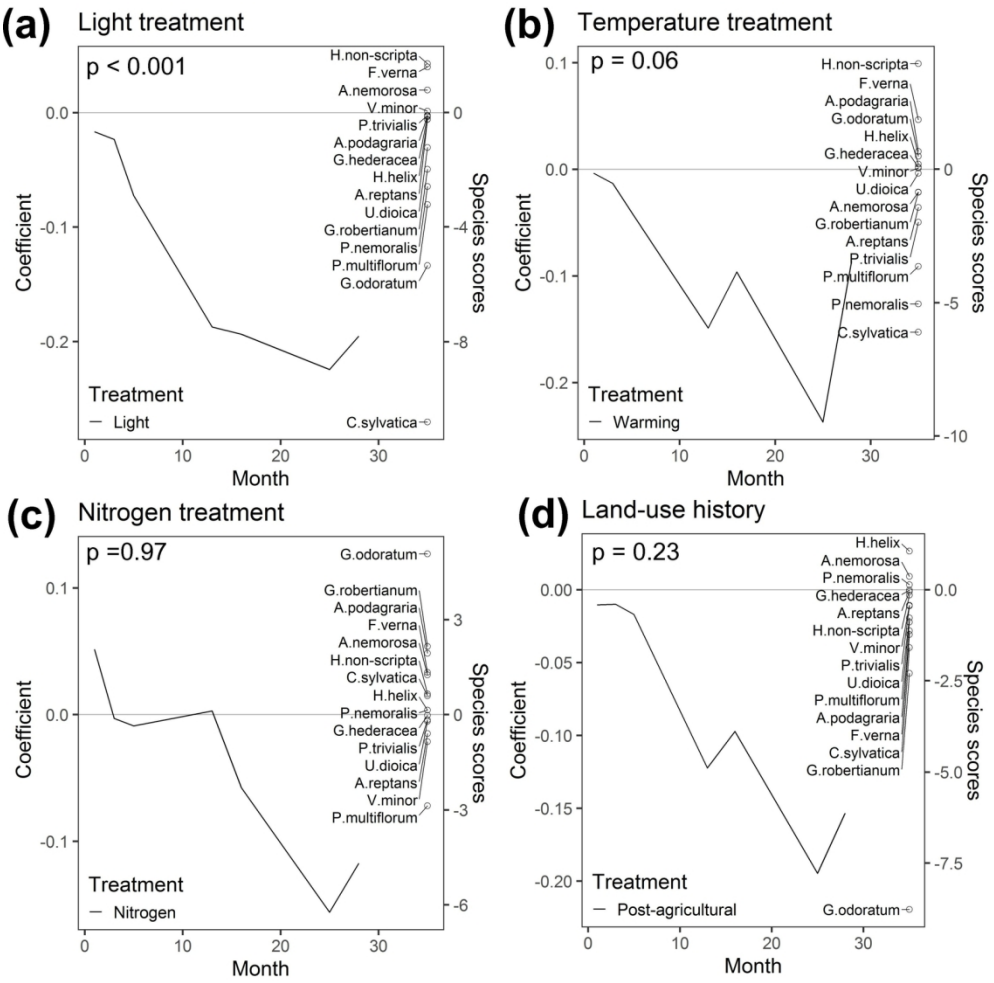

Figure 2: The light environment primarily determines abundance changes of species. Principal response curves of the light treatment (A), temperature treatment (B), N addition treatment (C) and the land-use history of the soil with ancient forest soil as control (D). Principal response curves show abundance changes of treated vs untreated communities using partial redundancy analysis (RDA) over time. Abundance changes in the control treatments are equated to zero. Multiplying the species score (right vertical axis) by the canonical coefficient of the RDA (left vertical axis) gives the relative abundance change of a species over time. Species that increase in abundance in response to the treatment have strong negative species scores, while species that decrease in abundance within a treatment are shown in opposite directions away from zero.

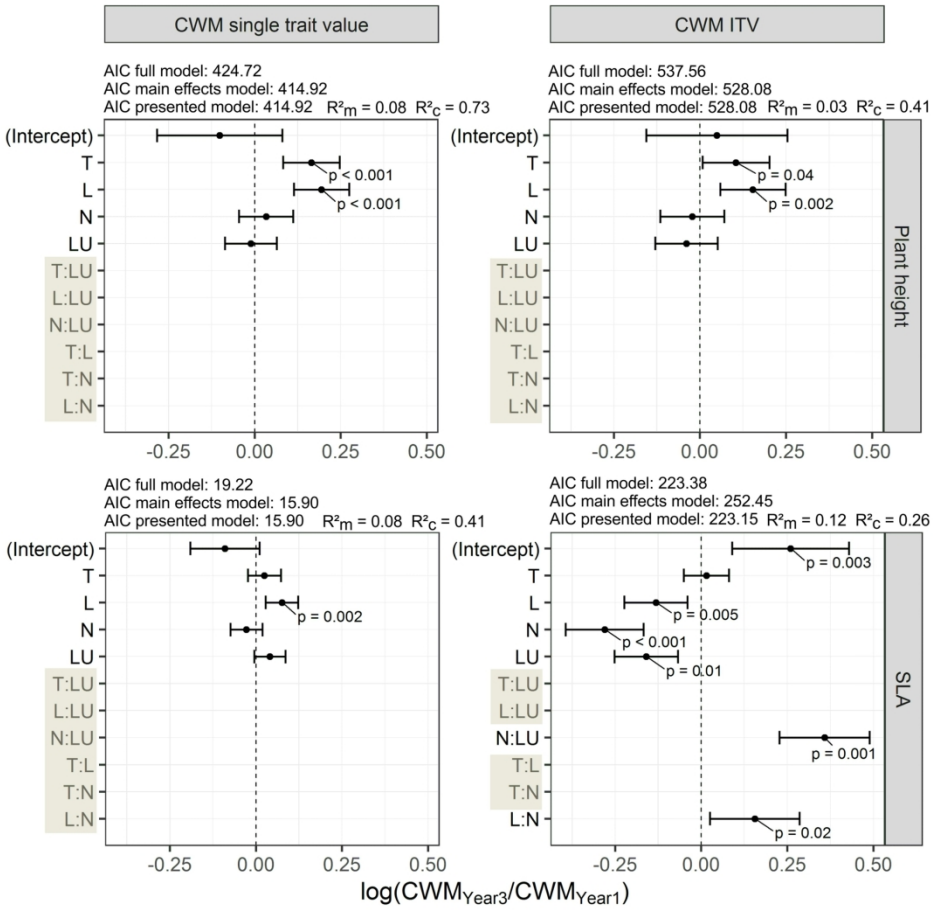

Figure 3: Light and warming are drivers for community plant height change over time due to species reordering, while SLA varies due to nutrient enrichment and light availability when considering ITV. Log response ratio of the community weighted mean (CWM) trait value in Year 3 over Year 1. The left panel for each trait has species reordering as the only source for CWM trait change ("single species- single trait approach"), while the right panels show the CWM value that incorporates intraspecific trait variation (ITV). The presented model was selected after backwards variable selection of the two-way interaction model of the temperature treatment (T), Light addition (L), N addition (N) and forest land-use history (LU, post-agricultural as effect relative to ancient). This presented model after variable selection includes all main effects and can include any significant interaction, which only occurred for CWMITV SLA. The comparison in AIC between the full interaction model, main effects only model and presented model (solution from selection procedure) is shown to support the model selection process. The model fit is given for the presented model, and includes fixed effects only ("marginal" R^2m) or with random effects included ("conditional" R^2c). P-values for factors are shown for significant effects only, see supplementary table S1.6 for detailed model summary output (including the Soil type covariate). The large difference in R^2m and R^2c is driven by the random effect term Community (12 levels, one for each species combination, see Supplementary Table S1.7). This difference in R^2 shows the importance of the initial species combination for determining a CWM of a trait value.

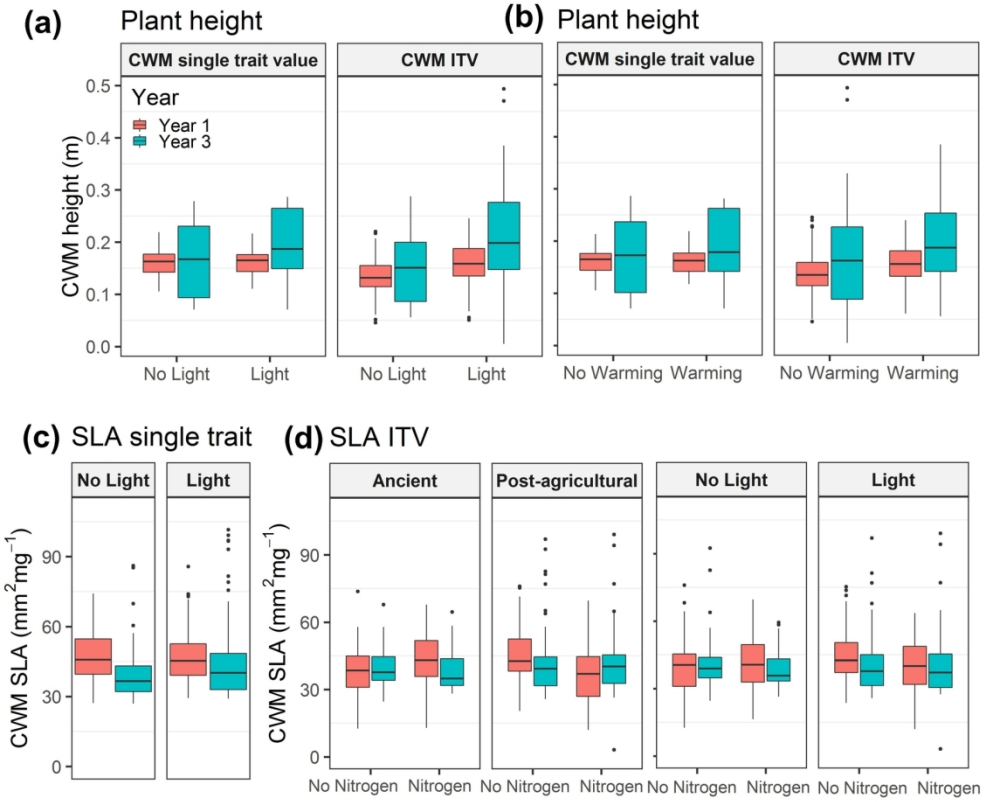

Figure 4: Community plant height consistently responds to light addition and warming due to species reordering, while SLA response changes with intraspecific trait variation (ITV). The boxplots on the interquartile range of CWM trait values are illustrations to the significant terms ($p<0.05$) from Fig. 3. We found the same significant effects of light (A), and warming (B) on plant height regardless of whether ITV was taken into account. CWM SLA responded to light in a single-species single-trait approach, but driven by some outliers (C). CWM SLA response becomes more variable when ITV is considered (D) as the effect of N addition depends on the land-use history and on light availability.